# Wild take for falconry and bird of prey genetics

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Natural England Technical Information Note TIN217

Richard Saunders, Senior Ornithologist

Donal McCarthy, Senior Project Manager

www.gov.uk/natural-england

# Contents

# Background

Natural England (NE) is responsible for determining licence applications to take native birds of prey from the wild (‘wild take’) in England for use in falconry and aviculture (hereafter referred to as ‘falconry’). Licences may be granted provided a set of licensing ‘tests’ are met. These tests include that there are no satisfactory alternatives, and no negative conservation impacts to the species concerned. Licences may only be granted on a selective basis and for a small number of birds.

Since the 1980s, and following substantial wild bird of prey population declines, the sector has relied on captive-bred birds. In recent years, however, and as wild populations of some species have recovered, there has been renewed interest in wild take and applications have been submitted to NE.

In early 2022, with the support of the Department for Environment, Food & Rural Affairs (DEFRA), NE launched a review to inform the development of a specific DEFRA wild take licensing policy based on the latest evidence, expert advice, and in-depth stakeholder insights from across the falconry and non-falconry communities. Wild take licensing was temporarily suspended to allow the review to take place.

Evidence has been gathered via a range of approaches including an 8-week public call for evidence, facilitated stakeholder workshops, semi-structured interviews with practicing falconers, engagement with academic experts and a literature review covering the cultural and historical aspects of falconry practice.

A key question that the review has sought to address is the extent to which captive-bred birds represent a satisfactory alternative to birds sourced from wild populations. Answering this has involved gathering evidence relating to, amongst other issues, the behaviour and genetics of captive and wild populations, respectively, to address matters such as the genetic health of captive stocks and the performance of captive-bred birds when trained for use in falconry.

This Technical Information Note (TIN) is one of the outputs of the review process. The aim of this TIN is to summarise NE’s understanding of the genetics evidence of relevance to the determination of wild take licence applications and hence a wild take licensing policy, and to consider whether any additional genetics work is required.

# Report structure

There are multiple different aspects to modern falconry practice, not all of which require detailed consideration from a genetic perspective. **Section 1** of this TIN considers which aspects do, and which aspects do not, require detailed consideration of genetics evidence in relation to wild take licensing. Aspects which it is concluded do not required detailed consideration of genetic matters include; i) wild take and subsequent release; ii) conservation translocations and reintroductions, and; iii) the risk of captive-bred birds escaping. Aspects which do require a more detailed consideration of genetic matters include; iv) the stated desire to fly birds that are a close genetic match to wild bird of prey populations native to Great Britain (GB), and; v) the potential for genetically-linked behavioural changes in captive populations that are detrimental to the performance of birds used for falconry.

A more detailed consideration of the relevant aspects of falconry identified in **Section 1** requires a basic understanding of certain genetic issues. **Section 2** provides a basic overview of relevant genetic techniques, and the factors by which it can be determined as to whether any genetic differences revealed by these techniques might be worthy of conservation or preservation.

**Section 3** considers information about wild GB bird of prey populations, and their genetic differentiation and hence distinctiveness, when compared to wild populations of these same native species in their non-GB ranges. The genetics of these wild populations are then considered in relation to the genetics of captive bird of prey populations. This section also summarises the findings of a key paper, which specifically compared the genetics of a regional GB Peregrine Falcon population to the genetics of both wild and captive Peregrine Falcon populations.

Finally, **Section 4** discusses the issue of potential behavioural change in captive populations, understanding the potential causes and considering possible remedies.

# Report conclusions

There is no clear evidence of a need for additional genetic input via wild take to maintain the genetic health of captive populations of the relevant species used to supply birds to falconers, or of a need for additional genetic input via wild take to establish new captive breeding populations from which falconers could source birds that share similar genetic characteristics to wild GB birds.

With the size of some captive populations exceeding wild GB populations by an order of magnitude, recent work suggests it is not fresh genes that domestic populations need, but better management of pedigrees (Puchala and others, 2021; Weaving and others, 2021). And, whilst a genetically distinct wild population of one GB bird of prey species exists at a regional scale, and other populations might be revealed by further study, there is no evidence that such populations will differ sufficiently from any of the described subspecies or races found elsewhere within the species' ranges to be elevated to a unique subspecies level deemed worthy of specific conservation or preservation efforts.

Finally, there is no evidence to demonstrate that genetic, rather than environmental factors, are the cause of any perceived inter-generational changes in performance between wild-taken parents and their captive-origin progeny when used for falconry. If changes in birds' performance were confirmed, regardless of the cause, the appropriate remedy is likely to be the same. Namely, that performance might be improved by a change in rearing methods and selecting desirable behavioural traits.

# Section 1: Falconry and genetics

## Aspects of falconry that do not require further consideration of genetics

There are no unresolved genetic issues relating to potential **wild take and subsequent release** as, hypothetically, any released birds taken under licence would be a genetic match to wild birds, when released back into the same wild donor populations from which they were originally taken. Therefore, this aspect of wild take does not require any further consideration of genetics.

Neither is there a need to investigate genetic issues relating to wild take for falconry and any subsequent link to **conservation translocations and reintroductions**. It has been suggested that a captive breeding programme, once established for falconry purposes, might then be expanded to benefit any future conservation translocation and reintroduction proposals that require donor stock for release. It is NE's view that the only wild bird of prey population that currently requires a captive breeding programme, to release their captive-bred progeny as part of a translocation project, is the Hen Harrier *Circus cyaneus*. The Hen Harrier captive breeding stock has been established by importing rehabilitated wild birds from France and Spain. It is NE's understanding is that this is not a species of interest to falconers and is not subject to potential wild take applications for the purposes of falconry and aviculture.

Other native bird of prey species that are either extinct as breeding birds in England, or subject to ongoing reintroduction efforts that have yet to result in the establishment of viable populations, include the White-tailed Eagle, Golden Eagle and Montagu's Harrier. Should new conservation translocation or reintroduction projects be set up for these species, captive breeding would not necessarily be the preferred avicultural option. Therefore, bird of prey translocations and reintroductions do not require any further consideration of genetic issues relating to wild take and captive-breeding for falconry purposes.

There is also no requirement at the present time to consider additional genetic evidence in relation to the potential risks to wild populations associated with **the escape of captive-bred birds of prey used by falconers.** It has been suggested that wild take is necessary to improve the genetic match between captive and wild populations of native bird of prey species, due to the risk of captive-bred birds escaping. Weaving and others (2021) estimate that each year *"30 peregrines and 30 peregrine hybrids...are lost and unrecovered by…UK falconers."* The number of lost captive bred birds are also reported by Fleming, Douse & Williams (2011). From 1983-2007, 687 registered Peregrine Falcons and 642 registered hybrid falcons were reported lost, reaching a peak of 57 lost Peregrine Falcons in 1993. With no requirement to report lost birds, these figures were considered an underestimate.

Escaped, genetically differentiated, falconers' birds might subsequently pair with wild birds. Concerns about potential anthropogenic genetic-introgression are mitigated, to a degree, as chance escapes are dispersed both temporally and spatially (Fleming, Douse & Williams, 2011). In addition, because escapes are akin to a hard release, many birds are expected to die within days (Fox & Chick, 2007). Other factors include the reduced fertility of hybrids (Eastham and Nicholls, 2005) and selection pressures operating against the survival of intermediate phenotypes (Kenward, 2009).

Despite falconers' birds escaping to the wild for many years, no non-native falconry species has yet become established in the UK (Fleming, Douse & Williams, 2011). Whilst the native Northern Goshawk has re-established (Petty, 1996), and isolated pairs of Eagle Owl have persisted for a few years (Melling, Dudley & Doherty, 2008), both of these are likely to have involved deliberate releases, rather than just accidental escapes. There is just a single example in GB of an escaped hybrid falcon breeding successfully with a wild Peregrine Falcon (Everitt & Franklin, 2009) and a single example from northern France of a female Peregrine x Saker hybrid breeding successfully with a wild male Peregrine Falcon (Cozic, 2016).

Whilst these events are rarely recorded and, subsequently, there is an absence of evidence relating to their impacts on population genetics, pairings involving phenotypically matched escaped and wild individuals of the same native species would be far harder to detect. Opportunities for study, to confirm evidence of absence of human-induced genetic-introgression, should be balanced by actions to prevent such pairings where known escapees are involved.

Finally, it is difficult to sustain an argument for licensed wild take to overcome the risk to native wild bird of prey populations posed by the potential escape of otherwise genetically differentiated captive birds, alongside the prevalent use of hybrids by British falconers where, by definition, a genetic match cannot be achieved. Indeed, the risk of escapes and genetic introgression has led to calls for the production of hybrid falcons to be banned in Europe, where the risk to IUCN red-listed (Endangered) Saker Falcon is particularly acute (BirdLife International, 2008).

## Aspects of falconry that do require further consideration of genetics

Genetic issues do need to be considered in relation to existing captive populations and the stated preference of some falconers to **fly birds that are a genetic match to native species' populations in the wild**. Determining a genetic match requires knowledge of both the genetics of wild native GB bird of prey populations, as well as the genetics of these same species' captive populations.

In addition, it has been purported that there is a **genetic link to the perceived lack of 'wildness'** experienced in F2[1] generations and above. Altered selection pressures in captivity could theoretically favour alleles that are maladaptive in a wild environment, thereby altering the behaviour of falconers' birds when being used for falconry purposes (e.g. hunting). This aspect does require further consideration of genetics.

Due to their popularity in falconry, Peregrine Falcons are likely to be the main species involved – this has been backed up via analysis of responses to NE's wild take licensing review call for evidence in 2022 (see **Annex A**). As its name implies, this species is one of the most widespread birds globally and the most widespread bird of prey. As a result of this extensive distribution, there are 19 subspecies recognised worldwide (del Hoyo, Elliott & Sargatal, 1994).

The other main species of interest is Sparrowhawk, one of the most numerous and widespread birds of prey in England. The most recent estimate (2016) of the wild population found in the UK is 31,000 pairs (BTO, 2023). Captive breeding and reintroduction have not been identified as a conservation need for this species and captive-populations are considered to be well-established (JNCC, 2023).

## Genuine need and falconers' views

When assessing applications against licensing tests, NE needs to understand whether there is a genuine problem or need and, in the absence of alternatives, whether the licenced activity would be a proportionate response to meeting, or contributing to, the resolution of this problem or need. The main genetic argument for further wild take appears to relate to the stated desire, amongst some falconers, to fly birds that they believe are a close genetic match to wild GB birds of prey, and the view that this is essential to preserve the cultural heritage of GB falconry.

A further consideration for a NE licensing assessment, is whether it is reasonably practicable for falconers to source birds from current captive stocks that share the characteristics of native populations (in terms of genetics and/or phenotype). Doing so might be challenging if there has been a large amount of hybridisation and/or if there has been poor monitoring and documentation, such that the captive population is not a reliable source.

If genetic differences do exist, would they adversely affect, or influence, the behaviour, morphology or performance of birds when used for falconry or avicultural purposes? If captive and wild birds exhibit the same phenotype, potential wild-captive differences might only be revealed by laboratory testing. Can this genetic issue be deemed an essential

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[1] F1 is the first generation of offspring from the parents. F2 is the second generation, obtained through breeding of F1 individuals.

cultural aspect of falconry, or is this just a niche interest – contradictory to the widespread practice of flying non-natives and hybrids (noting this would be a judgement for NE’s licensing team, rather than a technical genetics evidence matter)? Further evidence gathering by NE must nevertheless be proportionate, providing evidence to support a genuine licensing need, rather than seeking to meeting a philosophical desire or solve a problem which, at this stage, remains hypothetical.

It appears that many falconers are satisfied to fly birds sourced from captive stocks, including non-native and hybrid birds. A summary of falconers’ views obtained via the NE wild take review process are reproduced at **Annex A**.

# Section 2: Genetic Issues

## Species concepts

Biodiversity can be subdivided into categories from genes to ecosystems, but it is the species which is the fundamental unit of biology, ecology and conservation. It is species which are crucial to conservationists and policy makers and underpin both legislation and conservation delivery (Tobias and others, 2010). Species delimitation must therefore be consistent and transparent. It is not, however, straightforward. Subjectivity is introduced via individual preferences for different, yet instable and shifting, species concepts. Lineages diverge across evolutionary timescales, yet taxonomy requires organisms, potentially on a transition between populations and species, to be pigeon-holed in the present. Rapidly developing molecular analyses have improved understanding, yet simultaneously demonstrated that genetic divergence cannot easily be translated into species limits.

Since the formation of the **Biological Species Concept** (BSC) (Mayr, 1942) reproductive isolation has been the decisive criterion in the classification of birds. The ability of certain closely related species to hybridise, however, complicates interpretation of the central tenet of this concept in its original form. Del Hoyo & Collar (2014), provide a more flexible description of an avian species as follows: “An avian species is a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilisation system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems.”

Such reproductive isolation is easy to demonstrate where sympatry occurs. Even for species that are difficult to distinguish by appearance alone, despite individuals of the two species living side by side, there is no gene flow between populations. Separation of allopatric species can be more challenging, where geographic separation alone is insufficient to demonstrate potential reproductive isolation. The prevalent approach for allopatric species with very similar physical characteristics, is to compare the level of differentiation between the potential species pairing under scrutiny, with the level of morphological and vocal differentiation between two accepted, closely related, sympatric species (del Hoyo & Collar, 2014; Tobias and others, 2010). Within a GB context, the GB Ornithologists' Union's Taxonomic Subcommittee have species-defining criteria. Criterion 4.2 states allopatric taxa may be treated as species if “at least on character is fully diagnostic, and the level of divergence is equivalent to that of the most closely related sympatric species.” (Helbig and others, 2002). Nevertheless, the basis for elevating populations to species level (splitting) or downgrading (lumping), can be subjective and determined by personal preference for species concept.

Unlike the BSC, the cornerstone of the **Phylogenetic Species Concept** (PSC) is diagnosability (Cracraft, 1989). Rather than reproductive isolation, morphology, plumage, behaviour and increasingly vocalisations and can all be used to identify species (Tobias and others, 2010; del Hoyo and Collar, 2014). Once heavily reliant upon morphometrics of museum skins, technological advances in the recording and analysis of sound, have allowed taxonomists to increasingly use vocalisations to compare differentiation amongst bird populations. Diagnosability is problematic, however, as there is no clear limit as to how subtle a difference might be. As discussed by Tobias and others (2010), in tropical archipelagos or mountain ranges, there could be many tens of thousands of subtly divergent, sedentary populations diagnosable by at least one minor trait.

## Identifying subspecies

In well-studied bird of prey populations distributed in temperate climates, considering the presence of subspecies, rather than subtle differentiation and potential species limits, is more relevant to wild take and falconry applications. A subspecies is described as requiring a degree of genetic differentiation well above the level of genetic differences that exist among local populations. Smith, Chiszar and Montanucci (1997) quantify this genetic level, by introducing a threshold whereby two discrete populations are considered different subspecies if between population differences are greater than 25% or more of shared genetic variability.

Whilst this quantified genetic threshold might have provided a neat, clear limit, subsequent developments in taxonomy reveal a more complex picture. For example, phylogenetic work by Hackett and others (2008) revealed a sister relationship between passerines and parrots and corroborated previously contentious groupings, such as flamingos and grebes. The work by Tobias and others (2010) develops this approach further, using the BSC as the basis for their study and estimates of mean divergence to develop criteria for species delimitation, based on data-driven thresholds. In developing their criteria, Tobias and others (2010) focus on phenotypic evidence and set aside genetic data, as there is no widespread agreement on how genetic data can or should be used to delimit avian species (Winkler, 2010). As noted by del Hoyo & Collar (2016) groups of up to five clear species have proven genetically inseparable, whilst other species possess startling genetic divides that have no effect on their behaviour or status.

## Genetic techniques

Different genetic techniques would be appropriate to; i) compare wild GB and wild continental bird of prey populations; ii) compare captive and wild GB populations; iii) to determine the presence of hybrid genes in captive birds; iv) to check relatedness / possible inbreeding of captive birds and, finally; v) to explore a possible genetic link to any perceived behavioural change.

The use of mitochondrial DNA (mtDNA) testing could be used to compare wild GB and wild continental birds of prey and detect the presence of hybrid / mixed sub-species genes within captive birds. Use of mtDNA testing is relatively simple. mtDNA only represents a small portion of a birds genome and is maternally inherited, so would not be suitable to guarantee the absence of hybrid genes (of different species or sub-species) as these could be located in the nuclear DNA of a bird or inherited paternally. It can, nevertheless, provide a good indication of a bird’s ancestry

Analysis of nuclear DNA involves more complex testing providing a much finer level of detail, with an ability to identify individual level variation, rather than just using mtDNA to analyse a species via maternal lineage. Different tests involving nuclear DNA can present results that, without some explanation, might appear contradictory. For example, it is possible for the same captive individuals to be, simultaneously, genetically diverse yet also inbred.

Genome wide homozygosity / heterozygosity provides a measure of inbreeding. Specifically, homozygosity can be observed when there is only one variant at a locus in a microsatellite analysis. It is a measure of inbreeding (i.e. parents are siblings) with a higher level of inbreeding giving a higher inbreeding coefficient or fixation index. Heterozygosity describes the condition of having two different versions of a genomic marker or alleles (genes) from each biological parent; specifically, when there are two different alleles at a locus.

Genetic diversity is not the same as heterozygosity. Genetic diversity can be seen as the number of alleles and the number of private or ‘unique’ alleles for that group not seen in others. Therefore, there can be lots of different alleles in a genetically diverse population, including unique private alleles, but the majority could be homozygous, with only one variant at each locus, and with fewer heterozygotes than would be expected by chance. Therefore, although it might seem counter-intuitive, it is possible for captive falcons with hybrid DNA via different falcon species or subspecies, that would be a poor match for wild GB birds, to be genetically diverse but the offspring of close hybrid relatives, with high inbreeding levels. Some more detail about genetic terms necessary for consideration of wild take is provided at **Annex B.**

## Genetic differences worthy of preservation

It is possible to use nuclear DNA to identify individual animals so, clearly, it is possible to use genetic techniques to demonstrate differences between populations. The key question is whether genetic differences at GB level, or across regional sub-populations, are significant enough to constitute a sub-species, or be deemed worthy of preservation?

Wild GB Peregrine Falcon DNA has already been collected via buccal samples. Even samples of potential *calidus* or other unusual Peregrine subspecies recorded as vagrants, have been analysed by the Wildlife Forensics Lab at the University of Aberdeen – with little genetic variation found between Peregrine subspecies (M. Collinson 2023, pers. comm.). Peregrines are also one of the best genetically studied species worldwide, with over 100,000 nucleotide sequences in GenBank hosted via the National Center for Biotechnology Information.

Evidence submitted by Science and Advice for Scottish Agriculture (SASA)) to NE’s wild take licensing review call for evidence process showed that their own initial analysis of samples from wild Peregrine Falcons in the 2022 breeding season had identified *“*small genetic differences across populations within the UK.*”* However, they did then go on to note that *“*previous published studies have indicated significant genetic differences between UK and non-UK populations of the *F. p. peregrinus* subspecies of Peregrine Falcons.*”* (Nesje and others, 2000). The referenced paper notes that this species is distributed nearly worldwide but that some of these populations are genetically distinct. For example, the paper concludes that *“*Scottish Peregrines are clearly differentiated from the Scandinavian populations*”* and hypothesized that this may be due to their different migratory habits.

When populations are isolated, allopatric speciation can result in divergence and evolution of new species. Isolation in a GB context might not purely be the result of geography. For example, genetic differentiation might be due to a population bottleneck. Habitat loss, persecution and the effects of pesticide use have all contributed towards bird of prey population declines, and many GB species experienced a population bottleneck, some to just a handful of breeding pairs. In small populations, differentiation via genetic drift, with a reduction in allelic diversity, can then occur. When isolation has an anthropogenic cause, however, such potentially deleterious genetic differentiation might require remedy, rather than preservation.

As GB bird of prey populations have recovered from historic lows, both in terms of range and numbers, differentiation might be reversed as individuals from once isolated populations start to mix once more. Dispersal distances in birds of prey can be significant; a single study of dispersal in Peregrine Falcons in south-west England recorded a maximum natal dispersal (i.e. from natal site to first breeding location) for females of 287km (n=9). The same study revealed a maximum recorded juvenile dispersal distance of 2,435km, involving the recovery a male in Morocco that fledged in Somerset (Drewitt and others, 2021).

# Section 3: Wild and captive bird of prey populations

## Genetics of wild GB birds of prey

Firstly, to determine if there is a genuine problem or need to satisfy, it must be determined if there are genetically distinct GB bird of prey species that differ to described races / sub-species found elsewhere within species' global ranges. Currently, there are no recognised endemic GB bird of prey species. Neither do any of the English breeding bird of prey populations belong to a recognised GB sub-species. Several species do have recognised subspecies; indeed, there are 19 different subspecies of Peregrine Falcon worldwide (del Hoyo, Elliott & Sargatal, 1994) but GB and English populations belong to populations of the nominate subspecies found breeding within near continental Europe.

Historically, many GB bird of prey species' populations experienced severe population declines, typically due to the combined effects of habitat loss and persecution (Brown & Grice, 2005). Some species became regionally extinct (e.g. Common Buzzard, Peregrine Falcon), some species declined to just a few pairs (e.g. Golden Eagle), some were lost entirely as English breeding birds (e.g. Red Kite, Marsh Harrier), some were lost across the whole of the GB mainland (e.g. Hen Harrier) and, finally, some species were extirpated from the whole of GB (e.g. Osprey, White-tailed Eagle).

Some extant species' populations then experienced a partial recovery from historic lows before the effects of organochlorine pesticides in the mid-20th century resulted in further declines. Peregrine Falcon had declined to an unproductive population of no more than an estimated 30-50 occupied territories by the 1960s (Brown & Grice, 2005). From these historic lows, many bird of prey species have now recovered. Some species have approached carrying capacity, with more recent trends showing stable or negative trends (e.g. Kestrel and Sparrowhawk), whereas the Buzzard continues to expand its range and the more recently reintroduced Red Kite has the fastest growing of all UK bird populations (Heywood and others, 2022).

For those extirpated species that recovered following reintroduction, or accidental escape of falconers' birds, the genetics of English birds will be a mix of their Spanish and Swedish (e.g. Red Kite), Norwegian (White-tailed Eagle) and Scandinavian (e.g. Northern Goshawk) donor populations. Similarly, the genetics of extirpated species that experienced a natural recovery (e.g. Marsh Harrier and Osprey) will be derived from recolonising continental immigrants. Finally, the genetics of rare breeding summer visitors like the Honey Buzzard, Montagu's Harrier and Hobby (the latter two species with GB ranges at the northerly extent of species' global distributions), will be determined by the provenance of migrant recruits. The dispersal ecology of these bird of prey species reveal sympatry with nominate continental populations and so do not merit further genetic study in the context of wild take.

Therefore, the issue of potentially genetically distinct English bird of prey populations is restricted to species that declined but were never fully extirpated, and where subsequent recovery would have been driven primarily via recruitment, rather than immigration and mixing with continental populations. The main species in this category are Peregrine, Merlin, Kestrel, Sparrowhawk and Common Buzzard. Of these five species, it is the Peregrine Falcon that appears to be of greatest interest to falconers.

Up to date taxonomic notes on species and subspecies are compiled by Birdlife International and the extract for Peregrine Falcon, accompanying the Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world (Birdlife, 2020), is provided as follows:

“Formerly placed in separate genus, *Rhynchodon.* Genetic data indicate close affiliation to *F. mexicanus* (Nittinger and others, 2005) and to *F. fasciinucha* (White and others, 2013). Cosmopolitan distribution has led to naming of c. 75 subspecies, many of these on flimsy grounds, and majority no longer accepted. Subspecies *madens* has been elevated to species level under phylogenetic species concept by some authors (Hazevoet, 1995), but level of differentiation relatively low. Subspecies *pelegrinoides* often accorded species status (usually incorporating *babylonicus* as a subspecies), but is significantly variable in plumage (Rodríguez and others, 2011), and appears geographically and morphologically too indistinct a taxon to merit species status; in recent study, both *pelegrinoides* and *babylonicus* exhibited very small genetic difference from other forms, and indeed were as distant from each other as from any of the other subspecies sampled (White and others, 2013, White, Cade & Enderson, 2013); in addition, claimed sympatry with both *brookei* and *minor* without interbreeding in Morocco (Schollaert & Willem, 2000) seems unclear (White, Cade & Enderson, 2013). Genetic study of North American subspecies indicated that, although *pealei* is genetically well differentiated, individuals of *anatum* and *tundrius* are historically inseparable genetically (Brown and others, 2007); suggestion that latter be subsumed within *anatum,* however, requires further investigation. Subspecies *submelanogenys* poorly differentiated, perhaps better synonymized with *macropus.* Described form *kreyenborgi* (in the past considered a separate species) is in fact a colour morph of subspecies *cassini.* Subspecies *furuitii* originally given as *fruitii,* but spelling emended on basis of internal information (Dickinson & Remsen, 2013). Nineteen subspecies normally recognized.*”*

## Genetics of captive GB birds of prey

Having considered whether there are genetically distinct GB populations of birds of prey, and whether any such genetic differences should be preserved, it is necessary to consider the genetics of existing captive stock. Firstly, might the genetics of captive stock closely match, or are they identical to, the genetics of wild GB birds, or is there too much genetic diversity due to the introduction of hybrid genes and mixing of different races? Secondly, if captive individuals do match the genetics of wild GB birds, as founding stock was of native provenance and not subsequently bred with other races / hybrids, might these birds have too little genetic diversity, as they are limited in number and might already show signs of inbreeding? Work undertaken to date has confirmed domestic populations have a higher level of genetic diversity (numbers of alleles) than wild birds in the UK, presumably because they are a mix of subspecies and even species, but also a higher level of inbreeding (Weaving and others, 2021).

It is possible for captive breeding to help populations recover from severe population bottlenecks. Well-known avian examples include the Mauritius Kestrel, California Condor and Hawaiian Goose. The Mauritius Kestrel recovered from just 2 pairs (Cade and Jones, 2002) and now there are over 200 pairs (Groombridge and others, 2000). The California Condor numbered just 22 individuals in 1987, and now there are 300 free-flying individuals and 200 in captivity (Robinson and others, 2021). Finally, there were only 30 Hawaiian Geese in the mid-1900s yet, thanks to conservation action, there are over 1,300 individuals (Veillet, Shrestha & Price, 2008) and it can be commonly found in captive wildfowl collections in GB.

The success of these species' conservation programmes does not imply that recovery from such severe bottlenecks does not present a genetic challenge. For example, Groombridge and others (2000) noted that across all Mauritian Kestrel loci studied, allelic diversity fell by 55%, and heterozygosity by 57% and that, whilst the kestrel population recovered without the addition of new genetic variation (Groombridge and others, 2000), genetic deterioration may yet affect this population's long-term viability and remedial conservation strategies are needed to reduce the impact of inbreeding (Ewing and others, 2008). Nevertheless, with appropriate strategies and careful pairings, recovery is possible; despite having been extinct in the wild, the California Condor genome still shows a high degree of genome wide heterozygosity (Robinson and others, 2021).

When considering founder effects, inbreeding and the potential loss of genetic diversity, Jamieson (2010) recommends 20 founder-genome equivalents for avian reintroduction programmes. In contrast, the captive Peregrine Falcon population is many orders of magnitude greater than either this rule-of-thumb for founder-genome equivalents, or the low points involved for any of the three well-known avian conservation success stories. This would also be the case for captive Merlin and Sparrowhawk populations. The following information about bird numbers in captivity was provided by the Joint Nature Conservation Committee (JNCC) as part of their response to NE's public call for evidence launched to inform review of 'wild take' licensing for falconry and aviculture:

"For the period 01/01/2012 to 31/12/2022 a total of 8,931 A10s[2] have been issued for pure Falco peregrinus[3] with only 0.05% of these reported to be from a wild or unknown origin.

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[2] An A10 is a certificate to allow the sale or commercial use of a species listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora.

[3] An additional 2,333 A10s were issued for hybrid spp, including *Falco pelegrinoides* which was clumped with *F. peregrinus* following taxonomic changes adopted at COP19 (effective March 2023).

This data does not account for specimens that hold A10s issued by EU Member States (such documentation is accepted by the UK if valid for the holder to use) and that entered the UK prior to EU Exit. A further 680 birds have been registered on the Bird Registration Database (Schedule 4 WCA) maintained by APHA during the same time period. An additional 17 birds are held by Zoological Institutions using the Species360 (ZIMS) Database (Species 360, 2023).”

Not only is a captive population exceeding of 9,000 birds extremely large, but it is also larger than the total wild population of GB Peregrine Falcons, estimated to be 1,769 pairs in 2014 (Wilson and others, 2018), even accounting for a significant pool of non-breeding individuals. Furthermore, as noted by Fleming, Douse & Williams (2011), up to 21% of disabled wild origin birds taken into captivity have, subsequently, been captive bred so it seems that there should be little risk of inbreeding in the current captive ‘population’ overall.

The equivalent figure for pure Sparrowhawk is just over 1,500, and captive breeding of this species to multiple generation is also considered to be well-established by JNCC. The figures for Merlin and Goshawk are just over 1,000 and 10,000 respectively.

## The Sussex Peregrine Falcon Study

In 2020, NE assessed a licence application to take Peregrines from the wild to establish a breeding cooperative capable of supplying birds for subsequent use in falconry that shared “the characteristics of the native GB population of Peregrine Falcons”. To assess the application, it was necessary for NE to consider “the extent to which the native population of Peregrine Falcons have identifiable genetic or phenotype characteristics” and “whether these are distinct amongst the GB population or shared with a broader population that exists in other countries or regions.”[4]

Evidence from one study was provided by an author, pre-publication, showing genetically distinct populations based on geographic distribution within the *Falco p. peregrinus* subspecies. It was concluded, based on this best available evidence reviewed at the time, that “a genetically distinct native population is, on balance, likely to exist.” It was noted that “no evidence has been presented or found to the contrary.” This study (Weaving and others, 2021) was published a year later and compared both wild populations and domestics. The full paper has provided NE with additional relevant information since this 2020 licence assessment and is one of the most relevant genetic studies. It was referred to during NE’s call for evidence, but not all consultees interpreted the findings consistently.

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[4] For further information, see the licence determination record for the wild take licences issued by NE in 2020: Natural England issues licences for taking Peregrine Falcons for falconry - GOV.UK (www.gov.uk)

Sussex Peregrine Falcon populations were identified as genetically differentiated, compared to populations of *peregrinus* subspecies in Ireland, Germany and the *brookei* subspecies from Spain. In turn, all four wild populations studied were genetically differentiated from domestics. There was statistically significant genetic variance between populations, but still with sharing of alleles across populations. There was no signature of the population bottleneck experienced by GB Peregrine Falcons, which did not persist long enough for genetic erosion to occur (i.e. a reduction in genetic variance due to inbreeding with potential negative consequences). The study was able to confirm Sussex Peregrine Falcons were the same before and after the species' population crash, by comparing nucleic DNA obtained from the existing population, with nucleic DNA obtained via dated historic museum specimens. If there had been a signature of a population bottleneck, this might highlight a need to introduce new birds from other populations, rather than indicating that the signature was worthy of genetic preservation.

The microsatellite analysis in Weaving and others (2021) was restricted to 7 loci, but this was not deemed an unusual sample size for this type of genetic study (R. Vega 2023, pers. comm.). Increased genomic coverage (thousands of loci) would improve the accuracy of the analyses and could be obtained via a more advanced technique known as Restriction Site Associated DNA sequencing. Low coverage whole genome sequence analysis (LCGWS) has also since emerged as a powerful and cost-effective technique for population genomic studies (Lou, 2021). Finally, a new pipeline tool called GenErode has also been developed for this same type of application; to directly quantify the genomic consequences of population declines by comparing genome-wide data from pre-decline museum samples and modern samples (Kutschera and others, 2022). Nevertheless, for a study not involving RAD sequencing, LCGWS or making use of GenErode, however, this sample size of loci (n=7) is not unusual and, nevertheless, revealed statistically significant differences between the various populations. The study assumed alleles were neutral in terms of survival / reproduction.

Statistical significance in this context did not mean, as some consultees have interpreted, significance in conservation terms, such that any genetic differences identified need to be conserved. There can be statistically significant differences between different groups of peregrines that share lots of alleles. Rather, the results mean that the overall distribution of alleles among the various groups is not completely even. This is not surprising, as many species in the wild with multiple populations show some level of significant genetic differentiation, and this could be due to historical factors (isolation), restriction of gene flow (few migrants), philopatry (animals prefer to stay close to where they were born, or mate and nest close to where they were born), or a combination of factors. Neither does statistically significant differences between groups mean that a group is a 'pure' breed.

# Section 4: Behavioural Issues

## Perceived lack of wildness

Feedback from NE call for evidence process (**Annex A**) and engagement with falconers has provided information that some falconers consider captive-reared birds, derived from wild stock (i.e. parent birds taken from the wild as eggs / chicks), may sometimes fly differently to the progeny of birds that have been captive-bred over multiple generations. There also appears to be belief amongst some falconers that this perceived lack of wildness and associated changes in birds' flying behaviour is due to an absence of selection pressure amongst captive populations, and that the effects of this potential genetic drift might be reversed by wild take and help ensure that their birds' hunting skills remain sharp.

## Genetic and environmental causes

It seems unlikely there is a detectable genetic cause that might result in such rapid behavioural change between wild-caught birds and their progeny from generations F2 and above. An environmental cause seems a more likely contributory factor.

One of the most obvious differences in the environment to which wild and captive birds are exposed is the rearing process. Whilst all wild birds are obviously parent-reared, captive birds could be either parent-reared, or hand-reared, depending on the avicultural technique favoured by the individual falconer. The imprinting that occurs via hand-rearing is, by it very definition, a behavioural change due to then environmental conditions experienced by captive birds. In addition, if wild birds perfect their hunting skills during a narrow developmental-window, immediately post-fledging, differences in the behaviour of captive birds might persist over a birds' lifespan, despite an environmental, as opposed to a genetic, cause. Some falconers attempt to replicate this developmental phase through the process of hacking; captive-bred birds are released around the point of fledging, but with the continued provision of food to allow their subsequent capture. Not all captive-bred birds, however, will be hacked in this way and, for those that are, this form of enrichment might not fully match environmental conditions experienced by wild birds once parental care ceases entirely.

If there is a genetic cause resulting in behavioural differences between wild and captive birds, or genetics are a contributory factor, demonstrating epigenetic effects of a bird's environment on gene expression and consequently behaviour, as opposed to mendelian inheritance, might not prove to be a feasible subject for a study linked to licensing evidence requirements. A Genetic Association Study would be necessary to attempt to match DNA to different behaviours. Such a study could take several years and, despite this significant undertaking, might not provide a clear result. If changes in performance were confirmed, regardless of the cause, the appropriate remedy is likely to be the same, whereby performance might be improved by parent-rearing and selecting desirable traits.

Behaviour-based management, to ensure that captive-reared birds exhibit appropriate wild-behaviours, has been demonstrated to be key to the success of avian reintroduction projects (Roberts and Luther, 2023) and the same principles will almost certainly apply to the performance of falconers’ birds.

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# Annex A: Wild take licensing review – summary of genetic evidence and views

The genetic provenance of the birds that they fly is of stated importance to many falconers that responded to NE’s ‘wild take’ licensing review call for evidence. **Annex A** summarises the key issues raised as part of this call for evidence and the views of falconers/falconry organisations and non-falconers/non-falconry organisations. This includes evidence gathered via follow-up semi-structured interviews, workshops, and a commissioned literature review. Reports covering each of these in turn have also been produced and published on NE’s Access to Evidence pages.

- There is a stated desire amongst some falconers to fly birds that are a close genetic match to native populations in the wild and/or that share characteristics of native populations in the wild (e.g. similar behavioural/morphological/physiological traits, similar hunting abilities and size). NE has previously assessed applications to take birds from the wild to establish a breeding cooperative capable of supplying birds for subsequent use in falconry that shared *“the characteristics of the native British population of Peregrine Falcons, in terms of genetics and/or phenotype.”*

- Some falconers have stated that they are unable to source birds of the desired genetic provenance from current captive populations. The main barriers to sourcing the desired birds that were identified by respondents were poor record-keeping, historical mismanagement of captive-breeding stocks and a lack of coordinated studbooks. Evidence has been provided by JNCC on the estimated numbers of live, captive Peregrine Falcon, Merlin, Sparrowhawk and Northern Goshawk currently held in the UK. This has been derived from the CITES licensing database and the Bird Registration database maintained by APHA. However, this dataset is incomplete and, as such, a greater number of birds may currently be held in captivity than the numbers suggest.

- Many falconers consider there to be significant genetic differences between native GB bird of prey species populations in the wild and those found elsewhere within their native range. However, others noted that wild birds of prey from continental Europe have been shown to fly to the UK and rear young successfully, suggesting some degree of interlinkage. One non-falconer respondent involved in bird conversation noted that *“we know from colour ringing projects that while the majority of juveniles do not typically disperse great distances…a few individuals are known to have travelled much greater distances.”* Non-falconry organisations were also sceptical of any significant differences. For example, one stated they were *“not aware of any genetic evidence that shows British peregrines to be a distinct population”* and that they *“believe it very likely that peregrines in captivity…will come from a diverse range of genetic backgrounds.”*

- References were made to the paper by Weaving and others (2021) which sampled populations in England, Ireland, continental Europe and in captivity, as well as from England prior to the population crash experienced in the late 20th century.[2] The study found "low levels of genetic diversity" across all populations sampled as well as "low but significant genetic differentiation among all populations... indicating some level of genetic structure in European peregrines." See report section on **The Sussex Peregrine Falcon Study** for further details.

- Falconer interviewees tended to view bird lineage and traits as more important than genetics. They also considered there to be no such thing as a 'pure' GB Peregrine Falcon and argued that birds of British lineage can be readily sourced from current captive stocks.

- A literature review commissioned by NE identified few texts describing the importance of genetic issues to British falconers or exploring if there are any significant or distinct qualities relating to individuals of the same species that are native to discrete areas. The review suggested that these issues may be affected by the relative infancy of captive-breeding and noted that selective pressures may not have had time to manifest, albeit that they may not manifest at all if such populations are effectively managed.

- The findings of the falconry literature review suggests that interest in this topic amongst practicing falconers may be somewhat limited, not least given the common falconry practice of flying non-native birds and hybrids. On the latter point, Fleming, Douse & Williams (2011) note that in recent decades there has been "a substantial shift towards the production, through artificial insemination, of novel falcon hybrids… [which are] more desirable to falconers than pure-bred birds – they may be larger and faster than pure-bred specimens, be less prone to disease, be more desirable aesthetically and may outperform wild-caught or pure-bred falcons."

- Falconers were asked about whether they think there is sufficient genetic diversity in current captive populations in England. Of those 20 who answered, 35% thought that there was, whereas 55% did not. A number of falconers highlighted a lack of evidence on this question and drew attention to the lack of studbooks to document the relatedness of individuals within current captive populations, largely due to poor record keeping. For example, one falconer respondent to the call for evidence stated that:

  "Most of the species bred in the UK should be well represented genetically. However, as many breeders have not bothered to keep records, there may well be an inbreeding potential."

  Another stated that they had "not come across any adverse effects/illnesses/genetic faults in captive bred native raptors…nor heard of any" and another that "there is little evidence so far of genetic problems within most commonly held species."

A non-falconry organisation argued that there was a lack of evidence to support the idea that “licensed taking of a number of wild-bred…[peregrines]…will improve the species’ captive gene pool” and suggested that “falconers should provide evidence from a DNA database that the practice would indeed improve the peregrine’s gene pool.”

- Some falconers think that fresh genetic input from wild birds is needed to sustain healthy captive stocks of the relevant species. In some instances, this has been linked to concerns regarding behavioural issues with birds in such populations. Some falconers think that that introducing wild genes into captive populations is needed to ensure their health. For example, one stated that this:

  “…would benefit and improve genetic diversity and reduce the deleterious effects of small population size, that can lead to inbreeding depression and genetic drift, resulting in low fecundity and increased infant/chick mortality…This has been well documented in captive populations. The captive population of peregrine in the UK has been genetically diluted with breeding of closely related peregrine sub-species as a consequence of not being able to source pure native peregrine into the captive population*.”*

- Amongst falconer interviewees, concerns were raised that historical mismanagement of captive stocks – notably poor record-keeping and lack of coordinated studbooks – may lead to genetic issues in future if not addressed.

- Some falconers stated that they consider there to be behavioural differences between captive-reared birds derived from wild stock and the progeny of birds that have been captive-bred and reared over multiple generations when trained and used for falconry purposes. For example, some consider that birds derived from wild stock have superior hunting abilities. Many falconer and falconry organisations disagreed with this. For example, one falconry organisation stated that falconers *“*can be confident that generations of captive/domestic breeding have not altered the nature of the bird.” Likewise, one experience falconer stated that they had *“*worked with and seen many [captive-bred] hawks perform to astonishingly high standards in the field with no difference in appearance to the flight of a wild bird.*”*

  The extent to which this is driven by genetic differences is unclear.

- Of those falconers who participated in the more in-depth interviews, the majority considered there to be little difference in the performance or behaviour of captive-bred and wild-origin birds when trained for use in falconry. If birds are taken from the wild as fledglings and trained for use in falconry, most falconer interviewees considered that there will be little difference in their behaviour compared with their captive-bred counterparts. The literature review also concluded that the captive-bred birds are considered to perform to a high level of satisfaction.

- Many falconers responding to the call for evidence thought that there would be a conservation benefit to establishing captive breeding programmes for native birds of prey via wild take, for example to supply birds for those falconers who wish to source ‘pure’ GB peregrines. Less than 20% of non-falconers and non-falconry organisations answered yes to this question, with many arguing that birds should only be taken to establish captive breeding (and release) programmes where there was a clear and demonstrable conservation need.

- Many non-falconers and non-falconry organisations responding to the call for evidence were concerned about risks to the conservation status of wild populations associated with releases or escapes, primarily the escape of hybrid birds, but also the spread of disease.

# Annex B: Wild take genetics glossary

**Alleles** are different forms of the same gene and can be shared across populations.

**Allele frequency** is how common an allele is within a population (number of alleles of a certain type divided by the number of alleles of all types).

**Allelic diversity** usually decreases after a bottleneck because rare alleles will be lost.

**Epigenetics.** The study of how behaviours and environment can cause changes that affect the way your genes work. Unlike genetic changes, epigenetic changes are reversible and do not change a DNA sequence.

**Genetic drift** is a process that causes a population's allele frequencies to change from one generation to the next, simply as a result of chance. This happens because reproductive success within a population is variable, with some individuals producing more offspring than others. As a result, not all alleles will be reproduced to the same extent, and therefore allele frequencies will fluctuate from one generation to the next.

**Gene expression** is the process by which the information encoded in a gene that is used to direct the assembly of a protein molecule. It is a regulated process that allows a cell to respond to its changing environment.

**Homozygosity** is a measure of inbreeding (i.e. parents are siblings). FIS is an inbreeding coefficient or Fixation Index. It is the proportion of the variance in the subpopulation contained in an individual. High FIS implies a considerable degree of inbreeding.

**Mendellian inheritance** describes how certain traits are passed from parents to their offspring.

**Microsatellites** are regions of repeated sequences or Simple Tandem Repeats (STRs) of usually 2-6 nucleotides in length.

**Mitochondrial DNA** (‘mtDNA’) can be used to determine species and sub-species but is only inherited down the female line so would not be suitable to confirm absence of hybrid genes in male birds. It is a short compact and simple test. There is not much mitochondrial DNA variation between peregrine subspecies.

**Nuclear DNA:** Nuclear DNA (i.e. contained within the nucleus in chromosomes) involves more complex testing. Micro-satellite markers are nuclear genomic regions used in forensics / paternity tests etc. They are used in conservation genetics to identify metapopulations, migration & gene flow.

**Plasticity:** The ability of a single genome to produce different phenotypes. Plasticity is not always epigenetic, but a broader concept. A genetic association study is necessary to match DNA to different behaviours.

**Restriction Site Associated DNA markers**. RAD markers are involved in a type of mapping that can sequence much more of the genome (not used in recent peregrine studies).

**Subspecies:** A subspecies is defined as a breeding segment of a species that occupies a portion of the species' geographic range and that is measurably distinct in phenotype, genotype, or both, representing a level of biological organization below that of species.

## About Natural England

Natural England is here to secure a healthy natural environment for people to enjoy, where wildlife is protected and England's traditional landscapes are safeguarded for future generations.

## Further Information

This report can be downloaded from the Natural England Access to Evidence Catalogue. For information on Natural England publications or if you require an alternative format, please contact the Natural England Enquiry Service on 0300 060 3900 or email enquiries@naturalengland.org.uk.

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